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Research Article

Invasive grasses do not always exhibit superior and faster plant life-history traits in the introduced range than in the native range

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Abstract

Many invasive plants are larger, and produce more seeds in populations from the introduced range compared to those from their native range. Annual invasive plants might also benefit in their introduced range from fast germination, early seed production and shorter life cycles. Using three species of annual grass native to Spain and invasive in California (*Avena barbata*, *Bromus hordeaceus* and *Brachypodium distachyon* spp. complex), we tested the hypothesis that plants from the introduced range are not only larger and more fecund, but they also have faster life cycles than plants from the native range. Additionally, these plant traits are expected to vary along climate gradients, both in the introduced and in the native populations. Hence, we collected seeds from introduced and native populations across different climate conditions and then grew them all under a common outdoor condition. In support of our hypothesis, we found that *Avena* plants from the introduced range were larger, more fecund and had a shorter lifespan than from the native range. By contrast, *Bromus* plants invested less biomass in reproduction in the introduced range. In *Brachypodium*, seeds from the introduced range germinated later and flowering was delayed compared to the native range. These plants also produced fewer seeds and had a shorter lifespan in the introduced range. Genome size analysis indicated that *Brachypodium* plants from the introduced range are tetraploid while, in the native range, diploid and tetraploid individuals co-occur. We found some trait variation could be explained by climate differences amongst populations, but this was mostly within the native range, suggesting that our study taxa are not yet locally adapted to climatic conditions of their introduced range. Overall, our common garden experiment indicated that the invasion success of these annual grasses is not clearly associated with superior biomass, reproduction or fast plant life-history traits. For *Brachypodium*, polyploidy may play a role in its invasion success.

Key words: Clinal variation, common garden, invasive plants, lifespan, Mediterranean grasslands, phenology, polyploidy, range comparison

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Introduction

Many studies have found that plants from introduced populations grow larger and produce more seeds than those from the native range (Blumenthal and Hufbauer 2007). Increased plant growth and reproductive output can result from several

causes. According to the evolution of increased competitive ability (EICA) hypothesis, posited by Blossey and Notzold (1995), introduced plants have left behind their natural enemies (herbivores or pathogens) and evolve rapidly towards an increase in plant size and fecundity at the expense of reduced defence against specific natural enemies in the native range. Several meta-analyses have confirmed the generality of this trade-off although its magnitude depends on the response metric (Rotter and Holeski 2018; Callaway et al. 2022). Increased plant performance can also be due to higher resource-use efficiency in the introduced range (Mozdzer et al. 2013; Heberling et al. 2016) and/or enhanced association with mycorrhizae (Sheng et al. 2022). Differences may also result from adaptation to slightly different climates between native and introduced ranges (Bontrager et al. 2021). Regardless the mechanism, when grown in a common garden, descendants from introduced populations tend to perform better than descendants from native populations (e.g. Hierro et al. 2022).

Beyond plant size and reproductive output, other life-history traits can influence population performance in the introduced range (Lau and Funk 2023). Accelerated or extended phenology can enhance the invasive potential of introduced populations (Godoy et al. 2009a, 2009b; Wolkovich and Cleland 2011). Many invasive plants thrive after disturbances or after a pulse of resources (Davis et al. 2000). Under these circumstances, they may benefit from rapid germination to grab resources quickly after disturbance (Reynolds et al. 2001; Xu et al. 2019). Similarly, the onset and duration of flowering might differ between native and introduced ranges, evolving in response to different environmental conditions between ranges (e.g. Zettlemoyer et al. 2019).

The associations amongst traits evolving in response to release from natural enemies and those evolving in response to climatic differences might produce high-performance genotypes (i.e. genotypes that can maintain high fitness in multiple environments). The mix of evolutionary pressures could also result in high plasticity in invaders across environmental gradients, as found in a meta-analysis (Liao et al. 2016). Trait combinations could include both rapid germination and growth, as well as large size and reproductive output, resulting in populations that are highly successful across new environments (Matesanz and Sultan 2013). However, to our knowledge there are no studies comparing the full spectrum of life-history traits and events, from seed germination to senescence, between plants from multiple populations across native and introduced ranges. To investigate the evolutionary basis of life-history shifts between native and introduced ranges, plant descendants from both origins must be grown under common environmental conditions across their full life cycle.

Common-garden experiments comparing native and introduced populations provide a tool for examining variation across populations in life-history and demographic traits (Moloney et al. 2009). These experiments are necessary to tease apart whether traits depend on species origin rather than on species identity and also to test whether they are due to genetic or environmental differences amongst the locations of provenance of the seeds. A drawback of this approach may arise when the compared populations come from geographical areas with very different environmental conditions, because trait differences associated with the population origin may be masked by within-range local adaptation (Colautti et al. 2009; Lucas et al. 2024). One way to avoid this shortcoming is to compare plants from populations occurring across similar climatic niches, while controlling as

much as possible for vegetation type (Pauchard et al. 2004; Hierro et al. 2005). Alternativelly, testing for genetically-based trait differences between ranges may be complemented with the analysis of trait-climatic relationships across source populations (Hulme and Barrett 2013; Liu et al. 2020). It is expected that, if local adaptation is taking place, some traits and climate variables will co-vary. If climatic/trait clines in populations from the introduced range match those in the native range, it could be indicative of post-introduction adaptive evolution (Woods and Sultan 2022).

Besides sampling comparable spatial and environmental variation in the native and in the introduced ranges, other biases, such as range differences in plant ploidy level, may obscure interpretations of post-introduction evolution. Polyploidy is common in many successful invaders and several studies have shown that polyploid lineages of some groups have a higher probability of naturalisation than diploid ones (Pandit et al. 2011; Pyšek et al. 2023). Some experiments have also found introduced polyploids to produce larger plants and to be more fecund than native range diploids (Broz et al. 2009; Te Beest et al. 2012; Nagy et al. 2018). Therefore, in taxa known to have different cytotypes, simultaneous exploration of ploidy level of native and introduced populations is essential to understanding trait comparisons and evolution.

Mediterranean grasslands offer the opportunity to test for differences in life-history traits between native and introduced populations of invasive species from the same vegetation type and across a similar range of climatic conditions. For annual grasses (Poaceae), there has been a largely unidirectional introduction of species from the Mediterranean Basin to other Mediterranean climate-regions of the world as a consequence of the historical upheaval occurring after the Columbian Exchange (Casado et al. 2018). This is particularly true for Mediterranean annual grasses that have replaced extensive areas of native grasslands or forblands throughout the Mediterranean climate regions of California (D'Antonio et al. 2012). These invasions have caused major impacts to the native biota and also to economic and social systems (Stromberg et al. 2007).

In this study, we compared life-history traits of home and away populations of three widely-distributed Mediterranean climate annual grasses, native to Spain and widely invasive in California: *Avena barbata*, *Bromus hordeaceus* and *Brachypodium distachyon* spp. complex. These species co-occur and dominate in many grasslands in both ranges. Therefore, our study compares three functionally similar invasive species, an approach that is relatively rare in literature (but see Villasor et al. 2024). By growing plants from many native and introduced populations in a common garden in the native range, we assess how life-history traits differ between continents and whether trait-climate relationships are similar between the introduced and native ranges. The existence of climate-associated trait clines in the introduced range would be indirect evidence of trait evolution. Assuming some level of natural enemy escape in the introduced range, we hypothesise that plants from the introduced range will be larger and more fecund than those from the native range. However, plants in the introduced range may also be larger in response to more favourable climatic conditions. Given the noted high amount of disturbance typical of California grasslands (Schiffman 2000), we also explored whether California populations have faster germination and potentially faster life cycles than those from the native range. In parallel, we also tested for

differences in ploidy levels of *Brachypodium distachyon* spp. complex between continents (see Materials and Methods).

Overall, we predict under common-garden conditions: (1) larger plant size, higher fecundity and shorter life cycles in populations from the invaded range; (2) similar trait variation in both native and introduced range populations along climate gradients of the seed provenance locations; and (3) polyploidy in the introduced *Brachypodium distachyon* spp. complex populations.

Materials and methods

Study taxa

The study grasses *Avena barbata*, *Bromus hordeaceus* and *Brachypodium distachyon* spp. complex (named by their genus, hereafter) are common self-pollinated annual taxa native in Spain and introduced in California. *Avena* has its original area of distribution in the Mediterranean Basin and the Middle East and it is naturalised in Western areas of North and South America, as well as Australia. *Bromus* has a Palearctic native distribution and is introduced in many American, Australian and African regions. *Brachypodium* is native to European Mediterranean countries, the Middle East and Southeast Asia; its global area of introduction is not mapped, but it is documented in several non-European Mediterranean regions such as in California, Chile, Australia and South-Africa. In the sampling area, the three taxa co-occur in many localities (Suppl. material 1: table S1).

Extensive grassland surveys indicated that the cover of *Avena* and *Bromus* is significantly higher in the introduced than in the native communities, while the abundance of *Brachypodium*, where it is present, does not differ between ranges (Díaz et al. 2020). According to the California Invasive Plant Council (https://www.cal-ipc.org/), two of the three taxa (*Avena*, *Brachypodium*) cause moderate or severe impacts on ecosystem processes and native communities. *Bromus* is widespread, but with limited impact. *Avena* and *Bromus* have been in California for > 150 years (Garcia et al. 1989; Heady 1977, respectively), while *Brachypodium* appears to be a more recent introduction (1930–1950), based on herbarium records (Bakker et al. 2009).

In our sampling, we considered *Brachypodium distachyon* to be the single annual representative species of that genus because this is the only annual *Brachypodium* mentioned in the Cal-IPC inventory (https://www.cal-ipc.org/plants/inventory/). However, phenotypic, cytogenetic and molecular analysis indicate that, in the native range, *B. distachyon* is a species complex (Catalán et al. 2012) with three distinct species: *B. distachyon* (2n = 10, genome size = 0.631 pg/2C), *B. stacei* (2n = 20, 0.564 pg/2C) and their derived allotetraploid *B. hybridum* (2n = 30, 1.265 pg/2C). In the circum-Mediterranean area, *Brachypodium hybridum* has a distribution range and niche breadth similar to its parental species (López-Alvarez et al. 2015). Moreover, diploid and tetraploid taxa can co-exist in the same locality (Manzaneda et al. 2012). In this species complex, it is not possible to disentangle morphologically the taxonomic identity of individuals in the field. As we did not collect maternal lines of seeds, we cannot assign the ploidy level in our assayed plant individuals (see Seed collection section). However, we conducted genome size analysis to infer ploidy level of sampled populations.

Sampling localities and climatic differences between ranges

Potential seed sampling localities were preselected based on taxa distribution according to GBIF (https://www.gbif.org/es/) and the Cal-IPC inventory (https://www.cal-ipc.org/plants/inventory/). Our objective was to select localities with the same vegetation type and Mediterranean-type climate, although it was not possible to control for whatever the past vegetation had been in California as many grassy areas had previously been shrubland. Many studies have found introduced annual grass performance to be sensitive to increasing temperature, water availability and their interannual variability (Zavaleta et al. 2003; St. Clair et al. 2009; Sandel and Dangremond 2012). Therefore, we aimed for sampling localities with a similar gradient in mean annual temperature, precipitation and precipitation seasonality (defined as the CV of monthly precipitation) in the two ranges, according to WorldClim 2.0 (www.worldclim.org). In WorldClim 2.0, bioclimatic variables are derived from the monthly temperature and rainfall values for the period 1970–2000. However, because of logistic and permit constraints, we could not collect seeds in all pre-selected localities and, thus, the final climatic conditions between the two ranges were not as similar as initially envisioned.

There were significant differences in climate variables between the two ranges for all three species (Table 1). Mean annual temperature was significantly hotter in the localities sampled within the native range in Spain than in the introduced range in California, probably because there were more sampling localities in coastal areas in California than in Spain (Suppl. material 1: fig S1). Mean annual precipitation overlapped greatly, although there was a tendency for California localities to be wetter than localities in Spain, except for the ones where *Bromus* seeds were collected, for which there were no significant differences between ranges. Precipitation seasonality was 29% higher across the introduced range localities than the native range, with little overlap in values between the two ranges for any of the three species (Table 1). The three variables were not significantly correlated with each other (0.37 ≤ Pearson's correlation coefficient ≤ 0.44).

Table 1. Climatic seed sampling locality characteristics (mean ± SE) in the introduced range in California and in the native range in Spain according to WorldClim 2.0 (https://www.worldclim.org).

Species	Climatic variable	California	Spain	t-value	p-value
Avena barbata	Annual temperature	15.17 ± 3.11	17.44 ± 0.65	-5.95	< 0.001
	Annual precipitation	659.38 ± 209.62	525.33 ± 171.14	4.01	< 0.001
	Precipitation seasonality	92.99 ± 4.83	64.14 ± 7.36	25.96	< 0.001
Bromus hordeaceus	Annual temperature	15.58 ± 3.16	16.52 ± 1.88	-2.1	0.039
	Annual precipitation	651.08 ± 209.43	615.53 ± 106.57	1.24	< 0.001
	Precipitation seasonality	92.98 ± 4.39	69.02 ± 4.64	31.36	< 0.001
Brachypodium distachyon spp. complex	Annual temperature	14.37 ± 0.87	17 ± 0.78	-18.2	< 0.001
	Annual precipitation	732.92 ± 188.03	526.77 ± 115.28	7.54	< 0.001
	Precipitation seasonality	94.08 ± 4.53	65.75 ± 5.46	32.17	< 0.001

Seed collection

From March to June 2023, we collected seeds from each taxon from 12–15 localities in south Spain and in California (Suppl. material 1: table S1). In each locality, we collected a bulk sample of seeds from at least 100 plants per taxon randomly chosen within a 10,000 m^2 area to generate a representative sample of the population. In both ranges, sampled populations were at least 5 km apart and distributed along a coast-inland transect (Suppl. material 1: fig S1). In total, we sampled seeds from 40 populations in Spain (*Avena*: 12, *Bromus*: 15, *Brachypodium*: 13) and 41 in California (*Avena*: 14, *Bromus*: 13, *Brachypodium*: 14).

As soil disturbances, fire and restoration treatments might alter plant performance in Mediterranean grasslands, we selected localities with broadly similar land-use histories over the last 25 years. According to land-managers, these localities had not been burned, ploughed or cultivated for that period, but most had been moderately grazed by wild or domestic ungulates.

Seed performance

During November and early December 2023, we compared seed germination between ranges by germinating seeds from each population on filter paper in Petri dishes. We placed five 10 cm-diameter Petri dishes per population with 10 randomly selected seeds in random order in transparent plastic boxes in growth chambers. Chamber conditions were seven days of darkness at 5 °C and 60% relative humidity, followed by constant light, 20 °C and 60% relative humidity as these are the standard environmental conditions for plant germination from a wide range of Mediterranean conditions (Manzano-Piedras et al. 2014). The dishes were continuously saturated with distilled MiliQ water and dishes were randomly moved twice a week to avoid position effects.

We recorded germination every day until no germination was observed for a week. Seeds were considered as germinated when the radicle or coleoptile was visible. Once germinated, they were removed from the Petri dishes. By the end of the trial, non-germinated seeds were tested for viability with tetrazolium.

For each taxon, range and population, we calculated the cumulative percentage of germination (i.e. total germination), time to reach 50% germination (i.e. time to germination) and seed viability (total percentage of germinated seeds plus the percentage of non-germinated seeds that tested positive with tetrazolium). The tetrazolium (2,3,5-triphenyl tetrazolium chloride - TTC) test indirectly determines the respiratory activity of the seeds by reduction of the tetrazolium salt (Miller 2017). We conducted a slight piercing in the cotyledon and soaked seeds on a tetrazolium 0.7% solution overnight at room temperature. We considered seeds to be alive if the embryo was red stained after treatment.

Plant performance and phenology

On 11 December 2023, healthy germinated seeds were haphazardly chosen and planted in 5 × 5 × 12 cm tray containers filled with standard soil mixture (Gramoflor Blumenerde). Seedlings were grown in a greenhouse at < 26 °C and watered every two days to maintain soil moisture. Containers were re-randomised in the greenhouse racks once a week to ensure that all seedlings received uniform exposure to environmental conditions.

On 20 December, once true leaves were completely formed, we planted eight randomly chosen healthy seedlings per population in individual 2.5 l plastic pots. In total, the experiment had 648 pots from 26 *Avena*, 28 *Bromus* and 27 *Brachypodium* populations with eight replicates each. Pots were filled with the same gardening soil used for seedling growth and were placed outdoors at the Doñana Biological Research Station (Sevilla, Spain). Pot position was randomised every week. To avoid mortality, when temperature was over 27 °C (26-28 April, 9-10 May), plants were watered simulating a precipitation event of 5.42 l/m^2.

During daily censuses, we recorded the date that plants started to show fully extended flowering stalks. Each week, we counted the number and length of new flowering stalks, as well as the number of full seeds per stalk. For *Brachypodium*, instead of the number of seeds, we counted the number of spikes, after checking that it was positively related to seed number (Pearson $r = 0.851$, $p < 0.00001$, $n = 80$, Suppl. material 1: fig S2). We harvested plants when they did not produce any new flowering stalk for a week. At that stage, plants showed signs of leaf senescence. Vegetative biomass and biomass of all seed heads were weighed separately after drying at 70 °C for 72 hours. By the end of May, all plants had been harvested.

For each taxon, range and population, we calculated the total aboveground biomass, the vegetative aboveground biomass, the biomass of seed heads (i.e. reproductive biomass), the total number of seeds (or spikelets for *Brachypodium*) per plant (i.e. fecundity), the percentage of reproductive biomass to the total aboveground biomass (i.e. reproductive allocation); the number of days from seedling planting to first floral stalk production (i.e. time to flowering) and the number of days from seedling planting to harvesting as the length of the growing period for these annual taxa (i.e. lifespan).

Statistical analysis

For each taxon, we tested whether life-history traits differed between the native and introduced ranges with linear and generalised linear mixed models (LMM and GLMM) using the R packages lmerTest (Kuznetsova et al. 2017) and glmmTMB (Brooks et al. 2023).

Seed and plant performance response variables were total germination, seed viability, total aboveground biomass, aboveground vegetative biomass, reproductive biomass, fecundity and reproductive allocation. We used Beta, Gaussian or Poisson as the error distribution family according to data structure (see Suppl. material 3). All models included range as a fixed factor and population nested within range as a random factor. The interactions between range and three climate variables (mean temperature, annual precipitation and precipitation seasonality) were included to control for the effects of climate on differences in seed and plant performance variables, as well as to account for potentially diverging climate effects across regions. A significant interaction would indicate that climate is playing a different evolutionary role in the two ranges. Different models were created. Three of them included each of the climatic variables individually and the fourth included the three variables. We calculated the Akaike Information Criterion (AIC) for models without the climatic variables, models including each of the three climatic variables individually and models including all three climatic variables. In general, the best models (the most negative AIC) were those including single climatic variables and the AIC did not differ substantially between single models ($\Delta AIC \leq 2$). Therefore, we base our results on the models including single variables. Moreover, to account for

multiple testing, we adjusted p-values by applying a False Discovery Rate (FDR) correction to response variables measured in the same plant in the same test.

To test for differences in the timing of the life cycle (time to germination, time to flowering and lifespan), we constructed three separate mixed-effect Cox's Proportional Hazard models using the package coxme (Therneau 2015) with sampling day to seed germination, to plant flowering or to plant senescence (yes/no) as unit of analysis. The Cox model is a flexible semi-parametric model to analyse time-to-event data, such as experiments where measurements are taken periodically by counting individuals that go through the event. The advantage of this model is that it is not based on any assumptions concerning the shape of the underlying distribution of the regression (Romano and Stevanato 2020). We also constructed Kaplan-Meier germination curves.

For each taxon and trait, we also assessed if the variability across the mean population values differed between ranges with a Levene's test performed with the R package car (Fox et al. 2012). All statistical analyses were performed in R (R Core Team 2024). To construct the figures, we used the R packages ggplot2 (Wickham and Chang 2016) and ggeffects (Lüdecke 2018).

Brachypodium distachyon spp. complex ploidy level analysis

Inferred ploidy level and genome size (pg/2C) were quantified by flow cytometry in two *Brachypodium* plants per population from seeds collected in the native range in Spain and the introduced range in California.

Flow cytometric analyses were conducted at the Biology Research Services (CITIUS, University of Seville) using a Coulter CYTOMICS FC500-MPL (Beckman Coulter, Fullerton, CA, USA) equipped with a 20-mW argon-ion laser (488 nm). Fresh leaf tissue was collected from two young plants (5–10 cm in height) per locality, cultivated under outdoor conditions at the Estación Biológica de Doñana for two to three months. *Solanum lycopersicum* cv. *Stupicke* (1.96 pg/2C) was used as the primary internal standard (Doležel et al. 1992). Approximately 2 cm^2 of *S. lycopersicum* and 1.5 cm^2 of *Brachypodium* leaf tissue were co-chopped with a razor blade in a Petri dish containing 1 ml of cold LB01 buffer (Balao et al. 2009). The resulting suspension was filtered through a 30-µm CellTric disposable filter (Partec GmbH, Münster, Germany) and stained with 50 µg/ml propidium iodide and 50 µg/ml RNase. Peak means were determined through manual gating using CXP software (Beckman Coulter).

Data resources

The data underpinning the analysis reported in this paper are deposited in the Zenodo Data Repository at https://doi.org/10.5281/zenodo.17454149.

Results

Effects of range on life-history traits

There were few significant differences in plant life-history traits between geographical ranges (Fig. 1, Fig. 2, Suppl. material 3, Suppl. material 1: table S4). Differences occurred mostly in *Avena*, where plants in the introduced range

were on average 25.9% larger and 19.2% more fecund than plants from the native range (Fig. 1, Suppl. material 3). Seed germination of *Avena* was highly variable amongst localities, but not significantly different between ranges. *Avena* plants from seeds of the introduced range in California had on average an 11-day shorter life cycle than those from the native range in Spain (Fig. 2, Suppl. material 1: table S4).

In contrast to *Avena* populations, *Bromus* plant size and fecundity was unaffected by range. However, in the introduced range, *Bromus* populations produced 5.7% less total seed biomass and had 5.2% lower reproductive allocation than plants from populations of the native range (Fig. 1, Suppl. material 3).

Brachypodium plants from the introduced range produced 42.5% fewer spikelets than plants grown from native range seed (Fig. 1, Suppl. material 3). They also germinated and flowered later and had longer life cycles (Fig. 2, Suppl. material 1: fig S3, Suppl. material 1: table S4) than those from the native range.

In general, the three taxa showed a wide variability in life-history traits across populations within each range, but no consistent differences between ranges (Suppl. material 1: table S5).

Effects of climate on life-history traits

Plant and seed life-history traits were more dependent on precipitation than on mean temperature and precipitation seasonality in the locality where seeds were collected, but climate-trait relationships were not consistent across species (Suppl. material 2). Moreover, the interaction between climate and range was significant for some traits in some species. Overall, traits co-varied with climate in 15 out of 63 climatic variables × species × traits combinations tested, but the association was mostly significant in only one range (14 of 15) and more often in the native (10) compared to the introduced (5) range (Suppl. material 2).

In one case, the significant interaction between climate and range indicated that the slope of the climate-trait relationship was the opposite between ranges: in *Avena*, vegetative biomass decreased with precipitation in the native range, but increased in the introduced range (Fig. 3). The other significant effects of climatic variables in the introduced range indicated that, in California, precipitation decreased fecundity and reproductive allocation in *Avena* (as overall plant size increased) and increased vegetative biomass in *Bromus* (Fig. 3). Additionally, seasonality increased reproductive allocation in *Bromus* (Fig. 3). No association between traits and climatic variables was found for *Brachypodium* (Suppl. material 2). In sum, climatic associated trait clines were found in 25% of the climatic variables × species × traits combinations tested, but mainly in the native range.

Brachypodium distachyon spp. complex ploidy levels

Our results indicate that in the introduced range all populations are tetraploid, except in one locality with co-existing diploid and tetraploid individuals. In contrast, in the native range, there were monocytotypic localities with only diploid or only tetraploid individuals and mixed-ploidy localities (Suppl. material 1: table S2).

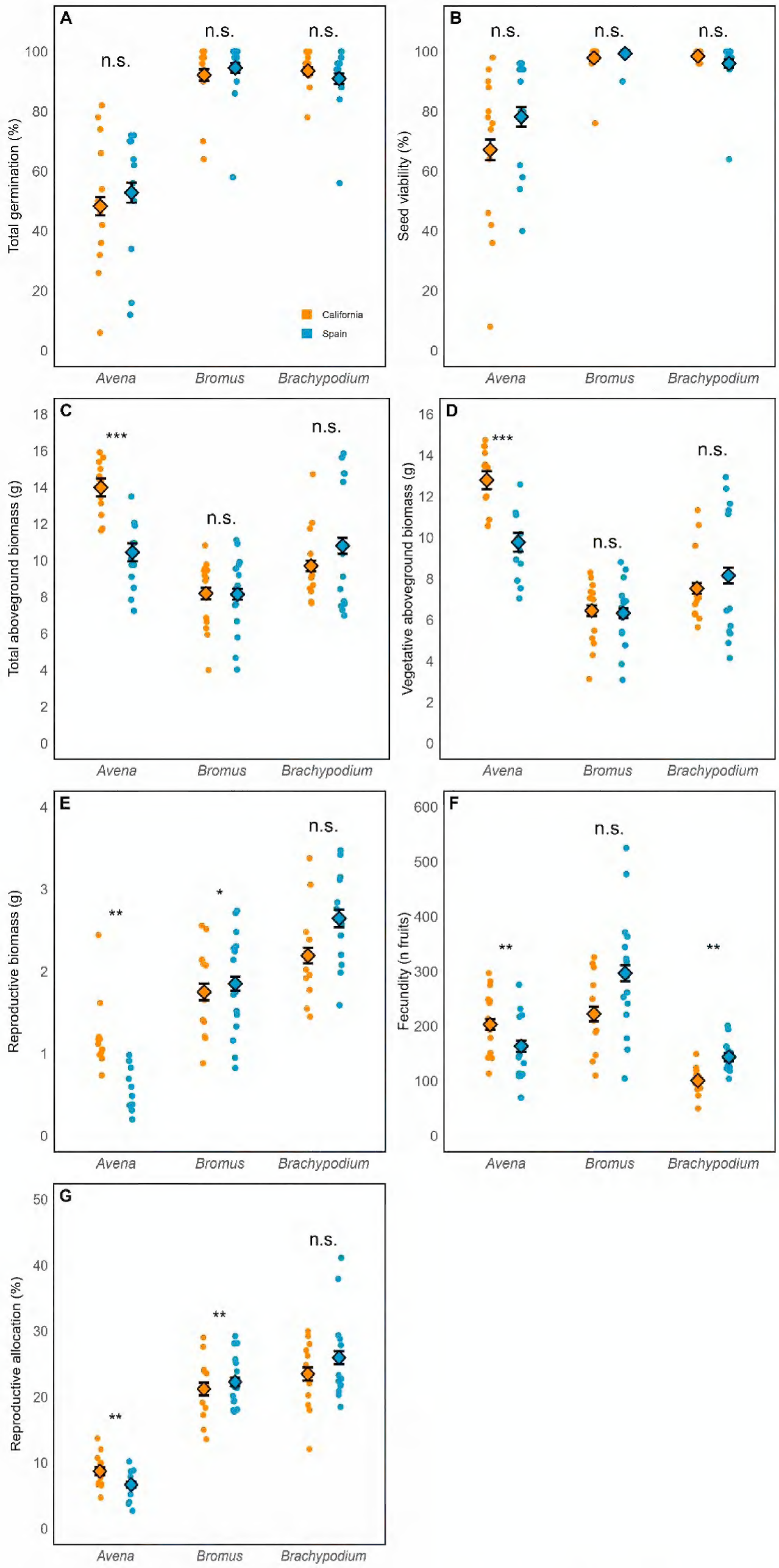

Figure 1. Seed and plant performance traits in populations from the introduced range in California and the native range in Spain. Dots indicate mean population values. Diamonds indicate mean values ± SE across the population means within each range. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

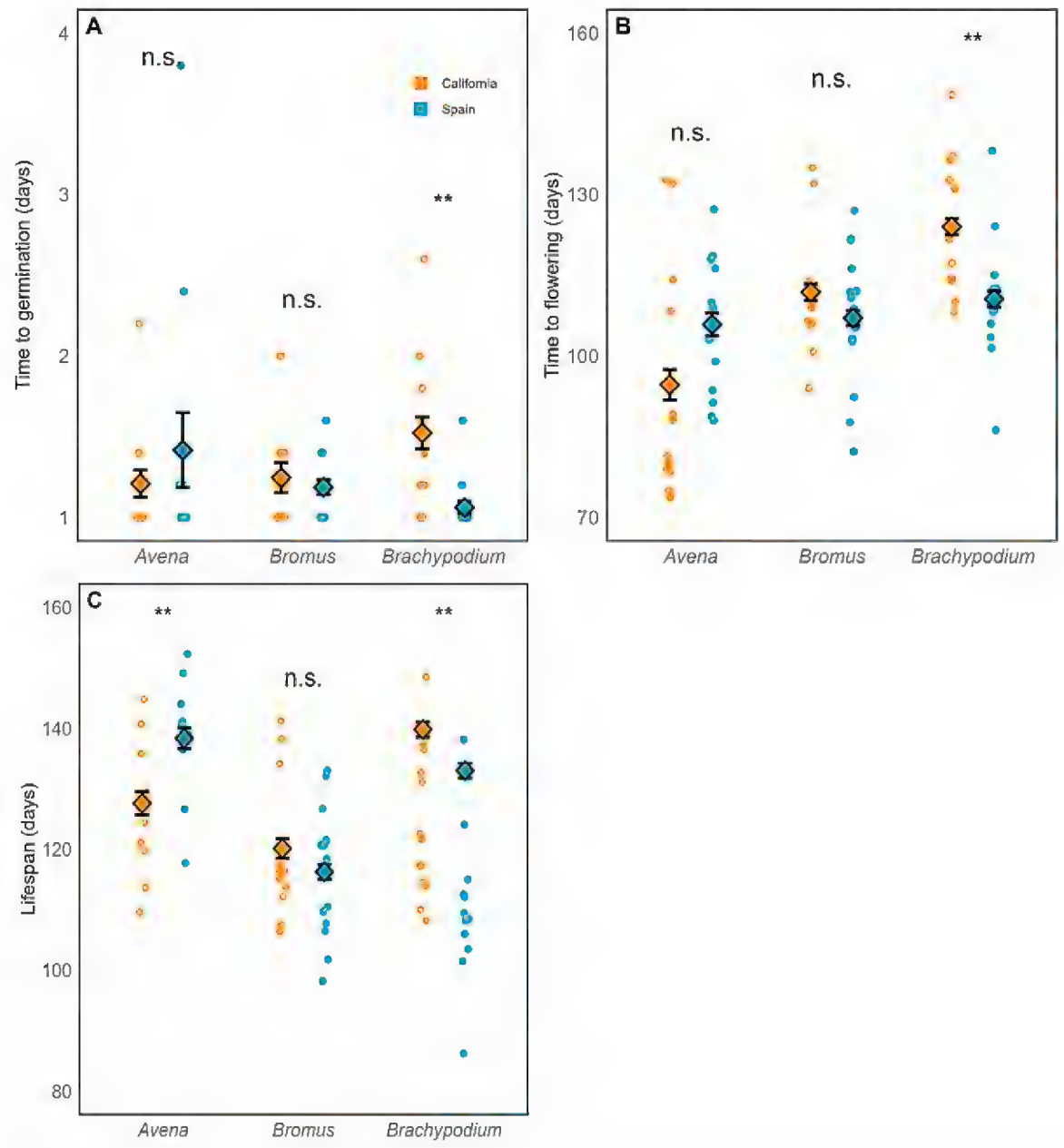

Figure 2. Phenology variables in populations from the introduced range in California and the native range in Spain. Dots indicate mean population values. Diamonds indicate mean values ± SE across the population means within each range. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

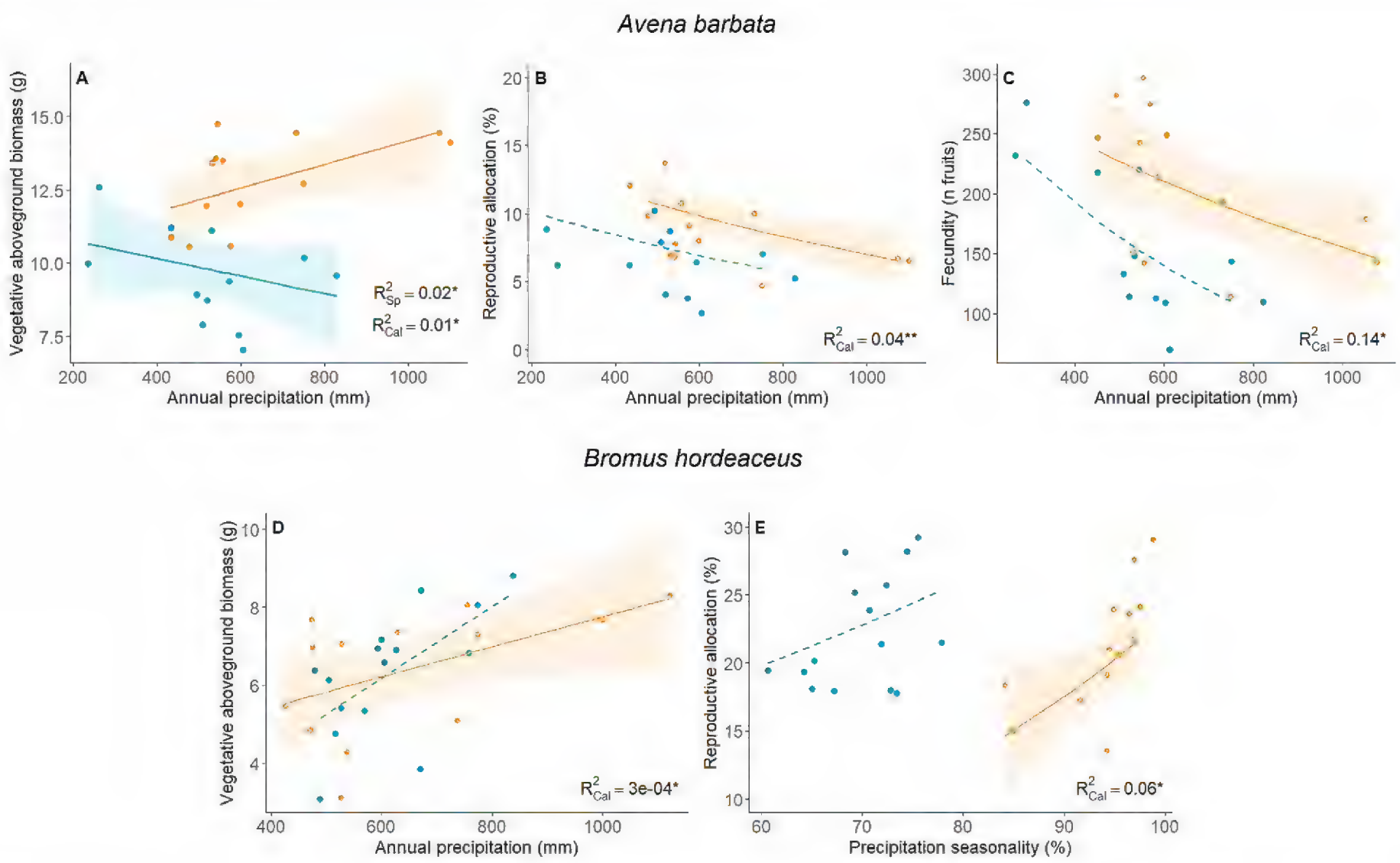

Figure 3. Contrasting life-history trait-climatic relationships in *Avena barbata* (top) and *Bromus hordeaceus* (bottom) in populations from the introduced range in California (orange) and the native range in Spain (blue).

Discussion

Our study goes beyond the one-species approach comparing native and introduced populations: we described the life-history traits in three grasses from native and introduced populations sharing the same vegetation type and across a range of different Mediterranean climatic conditions. In both ranges, the three taxa are widespread and locally abundant in moderately disturbed communities (Díaz et al. 2020). We predicted that plants from the introduced range would be larger and more fecund than plants from the native range, based on work done by others on native/introduced comparisons (e.g. Parker et al. 2013). Yet only one of our three taxa had significantly larger and more fecund plants in the populations from introduced range seeds. Therefore, even when testing our predictions on ecologically and taxonomically similar species (all annual Poaceae that thrive in disturbed Mediterranean environments), we found inconsistent effects of origin and climate on plant traits across species. Our results match those found in a study of three cool-season perennial grasses invasive in Canada, native to Europe: performance differences were inconsistent in magnitude or direction between native and introduced range plants (Villasor et al. 2024). This lack of consistency suggests that it will be difficult to find generalities in the search for which traits make plants invasive. Possible reasons for our results are discussed below.

Life-history trait differences

In our comparison of differences between plants from the native and the introduced range, we found that *Avena* was the only species to follow our predictions and show overall larger size, larger seeds and greater reproduction in the introduced range. The reverse was found in *Brachypodium* where fecundity was lower in the introduced than in the native range. Furthermore, the magnitude of the difference in seed production between ranges was much larger in this species than the one found in *Avena*. For *Bromus*, reproductive biomass and biomass allocation was also lower in populations from the introduced range. Therefore, in only one out of three taxa, plants from the introduced range performed better than in the native range. In our study, seedlings were planted into a common-garden in a rainy year so they did not experience water limitation, a key environmental factor influencing resource allocation patterns and phenology in Mediterranean grassland plants (Chelli et al. 2016; Nguyen et al. 2016). Assessing whether the lack of major differences observed was due to phenotypic plasticity, where differences would be stronger under different conditions, would require planting seedlings in contrasting environments.

Contrary to expectations, we also found no differences in total seed germination and timing amongst ranges, except for *Brachypodium*, which showed delayed germination in seeds from the introduced range. This contradicts results from several species in previous studies that found seeds from the introduced range germinated earlier and in higher numbers than those from the native range, under identical circumstances (Erfmeier and Bruelheide 2005; Beckmann et al. 2011). However, these studies also found that differences amongst ranges depended upon germination conditions and, as with growth conditions, these were not tested in our study (Notarnicola et al. 2023).

Climate versus range as drivers of variation in life-history traits

As the climatic conditions were distinct between ranges, trait differences may not represent between-range differences, but rather within range patterns of local adaptation to climate (Maron et al. 2004; Woods and Sultan 2022). We found some evidence for seed and plant life-history trait associations with climatic conditions. In the native range, some traits followed a climatic cline consistent with population adaptation to climatic conditions. For example, *Avena* plant biomass and fecundity increased with mean annual temperature or *Brachypodium* reproductive allocation decreased with precipitation seasonality. However, climatic associated trait clines were less common in the introduced range, perhaps because local adaptation has yet to occur. Other common-garden experiments have also found that among-population variation in life-history traits corresponds with the environmental conditions of source populations only in the native range (Villellas et al. 2021; Nagy et al. 2024). For example, *Conyza canadensis* populations from the North American native range are less affected by drought in populations from xeric than mesic habitats, but such relationships are not apparent for non-native populations from Europe, the Middle East and Asia (Nagy et al. 2024).

The lack of consistent clines between ranges can have different and not mutually exclusive explanations. It might indicate that, across the studied introduced range site gradient, populations have not adapted to the climatic conditions because introductions are relatively recent and there has not been enough time for the climate to act as a selection pressure in the face of what is likely a reasonably amount of gene flow (Sun and Roderick 2019). It might also be indicative of differences in the abiotic and biotic selection regimes between ranges. Possibly, similarities did not emerge because the climatic conditions from both ranges did not cover the same range of variation (Table 1).

The contrasting role of precipitation in influencing vegetative biomass in *Avena* between ranges suggests that different factors might be important depending on the range (Mayrose et al. 2011). In California, biomass increases with precipitation, as expected in an annual plant dependent upon seasonal rainfall and where the species is often a dominant in the annual flora. Yet the relationship is reversed in Spain; where precipitation is lower, sites are warmer and local diversity of native species is larger (Díaz et al. 2020). Possibly, in the native range interspecific competition is stronger than in the introduced range, a fact that could explain its lower local abundance and dominance compared to the introduced range (Díaz et al. 2020). If competitors benefit more than *Avena* during wet years or in wet sites, then *Avena* would possibly show a negative biomass response to rainfall, which is what we found. If competitive superiority in *Avena* in California derives from EICA, then populations from introduced provenances should be stronger competitors than populations from native provenances, a hypothesis that deserves further analysis. Future work should experimentally test how population differences in competitive superiority are modulated by warming and drought. Additionally, range differences might not be indicative of recent evolution in response to either climate or biotic factors, but a consequence of founder effects or pre-adaptation of introduced populations (MacDougall et al. 2018). Considering that we have only sampled seeds from a small part of the range of the species both at home and away, it is possible that trait differences already existed before introduction due to differentiation across the native range, rather than being the result of evolution after introduction.

Potential influence of polyploidy in *Brachypodium*

Our genome size results for *Brachypodium* align with those of Bakker et al. (2009) who found California seed accessions to be tetraploid and Eurasian accessions to be both diploid and tetraploid. They also found that, while *Brachypodium* is self-compatible and has a more recent introduction (1930–1950) to California than our other two species, the populations are genetically highly differentiated, showing a stronger isolation by distance than the Eurasian populations. The Bakker et al. (2009) findings suggest that *Brachypodium* was introduced in multiple locations within California with limited migration or genetic exchange amongst the locations. In contrast, the presence of co-existing diploid and tetraploid individuals in the native range might explain their larger variability in plant size compared to the introduced range.

Several other studies on invasive plant species have found polyploidy in the introduced range and multiple ploidy levels in the native range (Thébault et al. 2011; Te Beest et al. 2012; MacDougall et al. 2018). However, contrary to these studies, we have not found putative tetraploid individuals from the introduced range to perform better than putative diploid individuals from the native range. As mentioned in the Seed collection section, due to the difficulty of morphologically distinguishing different *Brachypodium* taxa in the field, we cannot assign correct ploidy levels to the essayed plants. Future studies should compare seed family variation of appropriate taxonomic groups of native and introduced populations (Lucas et al. 2024).

Conclusions

Poaceae are amongst the most widespread invasive taxa worldwide, responsible for substantial species compositional changes in grasslands and shrublands since European colonisation (Seastedt and Pyšek 2011). This is particularly evident in California (Rejmánek and Randall 1994) where repeated introductions of pre-adapted grass species might have occurred during more than two centuries of intensive lifestock grazing and land clearing (Stromberg et al. 2007; MacDougall et al. 2018). By comparing annual grass populations from the introduced range in California and the native range in Spain, we sought generality in understanding how invader traits might evolve across an introduced range. Yet, we found limited evidence for life-history advantages of the invasive taxa in the introduced range. Instead, our results did not apply uniformly across taxa.

In the introduced range, plants of *Avena*, the largest and most robust of the three species we studied, become larger and more fecund despite a shorter lifespan, while plants of *Brachypodium* produce fewer seeds and even delay flowering and grow more slowly. Climatic conditions in their area of provenance explained some of the trait variation across populations within ranges, such as vegetative biomass in the two ranges for *Avena*. Yet, the low number of climate-trait relationships suggests that climate is a relatively weak evolutionary pressure on trait evolution in these species as of yet. Population differences in life-history traits in annual grasses could also be related to polyploidy and its interaction with biotic factors, as has been suggested by others (Segraves and Anneberg 2016).

More complete testing for evolutionary adaption in the introduced range would require expanded sampling and experiments, including growing source populations under different environmental conditions rather than one ideal one (Lucas et al. 2024).

Likewise, to understand the mechanisms driving evolution of invaders in new ranges, future experiments should explore plant-plant, plant-herbivore and plant-soil interactions, and should compare cytotypes for polyploid taxa. Finally, ideally these studies should be conducted in both ranges, exposing the same maternal lines to the different treatments (Maron et al. 2004; Hierro et al. 2005).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

MV, CMD, JLF, IMP and PC designed the study; MV, CMD, JLF, IMP, AT and RM provided plant material; MV, AT and RM conducted the experiment; AT and RM conducted the statistical analysis; AR conducted the genome size analysis; MV wrote the first draft of the manuscript; all co-authors commented and revised several drafts of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text, the Supplementary Information and in the Zenodo Data Repository at https://doi.org/10.5281/zenodo.17454149.

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Supplementary material 1

Avena barbata, *Bromus hordeaceus* and *Brachypodium distachyon* – maps, results and analysis

Authors: Montserrat Vilà, Alejandro Trillo, Raúl Morón-López, Carla M. D'Antonio, Jennifer L. Funk, Ingrid M. Parker, Alba Rodríguez-Parra, Pilar Castro-Díez

Data type: docx

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Supplementary material 2

Trait-climatic variables relationships

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Data type: pdf

Explanation note: Contrasting life-history trait-climatic relationships in Avena barbata, Bromus hordeaceus and Brachypodium distachyon in populations from the introduced range in California and the native range in Spain.

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Supplementary material 3

Statistical analysis

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Data type: xlsx

Explanation note: Results of the LMM and GLMMs comparing seed and plant performance differences between populations from the introduced range in California and the native range in Spain.

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